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THE SIGNIFICANCE OF CERTAIN CHANGES IN THE TEMPORAL REGION OF THE PRIMITIVE REPTILIA.

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CERTAIN "mutations" or lines of definite evolution seem at the present time to be well established in the various mammalian phyla. Typical of such lines are the changes involved in the development of the Perissodactyla and Artiodactyla from the pentadactyl forms of the Eocene; the development of the complicated carnivorous and herbivorous molar teeth from the simple tritubercular type and the gradual assumption of the molariform condition by the premolars of the herbivorous forms. Around such persistent lines of development have gathered the minor changes or "variations" determining the various genera and species.

As yet there has been no recognition of such a line of definite evolution among the Reptilia, but it is the belief of the author that such a line can be demonstrated. The series of changes alluded to are those involved in the development of the temporal region of certain of the Permian Reptilia. Closely connected with this series are other changes, such as the gradual assumption of the tuberculate condition of the teeth and the introduction among the tarsal bones of a calcaneum.

The Pareiasauria Seeley (Cotylosauria Cope) are undoubtedly the most ancient of known Reptilia. The resemblance of these forms to the Amphibia demand that they be removed from union with the remaining Permian Reptilia in the group Anomodontia and considered as the ancestral form from which the Proganosauria have been derived, not the reverse, as suggested by Haeckel. The most perfect form of this group known is *Pareiasaurus bombidens* O. The cranial characters in which this form resembles the Labyrinthodonta are thus summed up by Seeley (1). "The head shows five Labyrinthodont characters: (1) the form; (2) the sculpture of the cranial bones; (3) the arrangement of the bones that cover the head; (4) the presence of mucous canals between the orbits and nares; (5) the absence of the lachrymal bone from the anterior corner of the orbit of the eye." To this evidence may be added the presence of a cleithrum, figured by Seeley as an epiclavicle (2). The presence of a cleithrum in the Pareiasauria is confirmed by the evidence of an isolated scapula belonging to this group from the Texas Permian, now in the museum of the University of Chicago. To the upper end of this scapula is attached the distal end of an element that can only be a cleithrum.

From the Pareiasauria arose the Proganosauria by a series of changes involving the appearance of two fossæ in the temporal region. The first appeared between the squamosal-parietal and the prosquamosal-postorbital, the second and lower between the prosquamosal-postorbital and the quadratojugal-jugal. This resulted in the formation of two temporal arches, an upper, the postorbital, and a lower, the jugal.

In describing the quadrate of Pareiasaurus, Seeley says (2), page 325, "the quadrate bones are vertical, compressed, oblique plates, which extend outward and backward. They are five and one-half inches high, and in contact throughout with the external temporal shield." A figure of a quadrate is given by the same author (3), which he refers "to Pareiasaurus or a near ally"; this figure shows the characters mentioned above. The American forms of this group show the same form of elongated quadrate.

In Paleohatteria, one of the earliest of the Proganosauria, we find the same elongate quadrate. Changes in other regions of the body, the tarsus, abdominal ossicles, and distal end of the humerus, gave rise to the Rhyncocephalia. The temporal regions of Proganosauria and Rhyncocephalia are very similar, the only difference being that in the first order the squamosal and prosquamosal are separate, while in *Sphenodon*, a typical rhyncocephalian, they are united. The condition of this region in the two forms is indicated in Fig. 1.

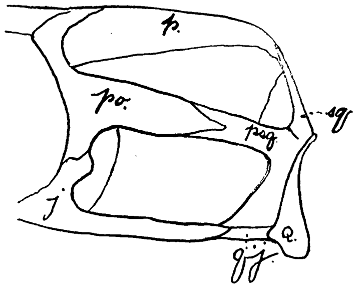


FIG. 1. — TEMPORAL REGION OF THE SKULL OF SPHENODON.

j, jugal; *p*, parietal; *po*, postorbital; *psq*, prosquamosal; *Q*, quadrate; *qj*, quadratojugal; *sq*, squamosal.

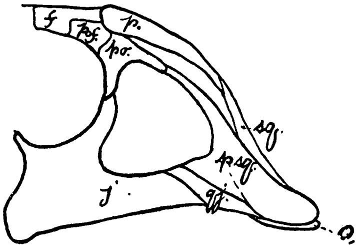


FIG. 2. — TEMPORAL REGION OF THE SKULL OF DIMETRODON.

f, frontal; *pof*, postfrontal. Other lettering same as in Fig. 1.

Before the development of the Rhyncocephalia, however, there appeared among the early Permian reptiles forms which exhibited the first steps in one of the most profound mutations of the reptilian line. These forms show a flattened form of quadrate instead of the elongated form of previous orders. It has been shown by Baur and the author (4) that the Pelycosauria of Cope are very similar in structure to the Rhyncocephalia, differing chiefly in the flattened quadrate. The difference in the temporal region of these forms from that of the Rhyncocephalia can be readily seen by comparing Fig. 2 with Fig. 1.

In the paper just cited, page 113, the authors stated that they considered the Pelycosauria "a specialized side branch of a line leading from the Proganosauria to the Rhyncocephalia." The author is now inclined to attach much greater importance to the appearance of the flattened quadrate at this point. The Pelycosauria and many of the Permian forms from South Africa and Russia all show this character of a depressed quadrate more or less completely surrounded by the supporting bones. They seem to form a definite group, with this feature as the common point in their structure. The quadrate is not equally depressed in all forms, nor equally surrounded by the bones of the temporal region. Thus the ancestors of the Pelycosauria were in all probability forms lacking the elongate neural spines characteristic of this group, with the quadrate distinct from the surrounding elements and not so much depressed. These forms are as yet unknown. The Pelycosauria are no longer considered as a side branch of the main reptilian line, but as one member or branch of an equally divided line leading from the Proganosauria.

From this point onward the Reptilia are divided into two groups, one with an elongate quadrate which includes all modern and most extinct Reptilia, and one with a depressed quadrate reaching its highest development in the Permian, and in all probability losing its identity by almost imperceptible stages in the direct ancestors of the Mammalia.

Haeckel, in his *Systematische Phylogenie* (Vertebrata), page 299, has grouped the Permian forms under two orders, the Theriodontia (*Mastocephale theromoren*) and the Anomodontia (*Chelycephale theromoren*). In the first order he places the suborders Pareiasauria, Pelycosauria, and Palatosauria; in second the Dicynodontia and Udenodontia. If it be true that the Pareiasauria are a distinct order they must be dropped from this group. Then the remaining suborders, as defined by Haeckel, comprise the forms possessed of the depressed quadrate. It has been shown by Baur and Case (4) that the group Theromora does not exist, and it is now suggested that the forms with the depressed quadrate be referred to as the mastocephalous Reptilia, because of their evident culmination in the Mammalia, while the remaining Reptilia may be described as saurocephalous. In no known form, so far as I am aware, is there a tendency for a member of one of these groups to assume the form and condition of the quadrate characteristic of the other.

Leaving out of consideration the aberrant Dicynodontia and Udenodontia, a steady progress can be traced from the primitive pelycosaurian forms to the mammal-like forms. The quadrate of the early forms, while flattened and covered to a considerable extent by the squamosal and prosquamosal bones, still shows to a considerable extent on the side of the skull; in the succeeding forms the quadrate is more and more reduced and the squamosal approaches more and more to an articulation with the lower jaw. Accompanying these changes are certain others, indicated below:

Pelycosauria: Quadrate depressed, appearing on side of skull. Teeth simple. Two well-developed arches.

Procolophonia: Quadrate depressed, nearly covered by the greatly enlarged quadratojugal (?). Teeth simple, reduced in number. Arches approximated only, a small foramen existing between the upper and lower.

Cynodontia: Quadrate covered by supporting bones. Teeth showing small lateral tubercles. Arches more closely approximated than in Procolophonia.

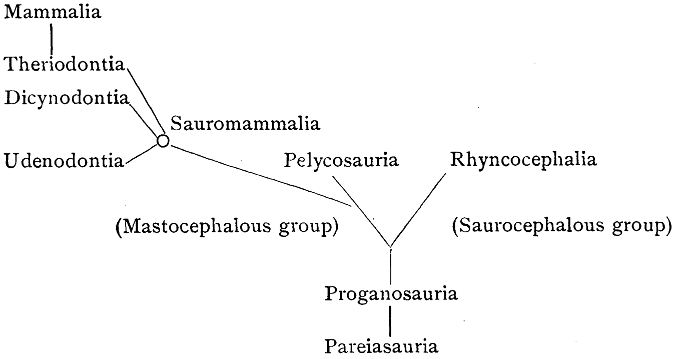
Lycosauria: Quadrate small, covered by supporting bones. Skull depressed. Teeth with well-developed tubercles. Arches united.

Gomphodontia: Quadrate very small, and inclosed in squamosal. Teeth tuberculate. Palate mammalian. Arches united.

The author was at one time undecided as to the nature of the arch in the Lycosauria and Cynodontia; in connection with Baur he said (4) that the mode of formation of the arch was uncertain. A specimen of *Cynognathus crateronotus*, figured by Seeley, shows an opening between the upper and lower arches which was uncertain in origin, there being some reason to suppose it to be the result of an injury to the specimen, but a study of the figure of Procolophon, given by Seeley, shows the same condition. The enormous quadratojugal (called squamosal by Leydekker) joins the jugal in front, which in turn joins a slender element by its anterior superior corner; this element runs backward, forming the lower and back portion of the orbit, and is undoubtedly the postorbital. Behind this element is another bone, the squamosal, or squamosal + prosquamosal, which rests upon the quadratojugal below; between all these elements is a small cavity, exactly as in Cynognathus. It is hardly probable that a break would occur in the same place in the two specimens, and so they are considered as showing the final stages of the union of the two arches to form the mammalian zygoma. This fact is further borne out by the very evident union of the two arches in Placodus and Cyamodus.

If this is true, the Theriodonta (Cynodonta + Lycosauria + Gomphodonta) cannot be the ancestors of the Squamata and Sauropterygia, as suggested by Cope (5). In these forms the history of the arches is very different. The Squamata possess only the superior temporal arch.

It is readily seen that the scheme here offered differs very little from that suggested by Baur in 1887 (6). The chief differences are the placing of the Pareiasauria as the most primitive group of the Reptilia, and the position of the mastocephalous Reptilia in opposition to all the remaining Reptilia, the changes in the quadrate region being the determinate feature in both groups. The following diagram will serve to make clear the ideas here expressed.



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